

INVITED PAPER*

Dams, zebras, and settlements: The historical loss of freshwater mussels in the Ohio River mainstem

G. Thomas Watters¹ and Carol J. Myers Flaute²

¹ Department of Evolution, Ecology and Organismal Biology, The Ohio State University, 1315 Kinnear Road, Columbus, Ohio 43212, U.S.A.

² College of Environment and Design, The University of Georgia, Athens, Georgia 30602, U.S.A.

Corresponding author: Watters.1@osu.edu

Abstract: The decline of the freshwater mussel fauna of the Ohio River, U.S.A. is compared to the dates of service of the existing dams, the arrival of the exotic zebra mussel, and the presence of urban centers on the mainstem. Based upon historical records we know that most pools supported 20-50 species of mussels; today many have fewer than ten. The results presented here show a mixed effect of the dams on the mussel fauna, ranging from marked deleterious effects in Hannibal, McAlpine, and Smithland pools to comparatively little effect in pools such as Dashields, Greenup, and Markland. In nearly all cases, the most dramatic declines in mussels were associated with the arrival of zebra mussels in the Ohio River in 1991. Pools with significant urban centers often had a loss of diversity well before the construction of dams or the arrival of zebra mussels; these losses are attributed to water quality problems associated with urban centers. Mussel diversity has thus declined in the Ohio River as the result of a three-fold problem: loss of water quality, existing dams, and zebra mussels.

Key words: Unionacea, diversity, impoundments, Dreissenidae, water quality

"The Ohio is the most beautiful river on earth. Its current gentle, waters clear, and bosom smooth and unbroken by rocks and rapids, a single instance only excepted" (Thomas Jefferson 1782: 256).

The Ohio River system is one of the largest in the world (1,579 km long with a watershed area of 490,603 km²). It was an important navigational route for both Native Americans and European settlers. Forts were established on the river by the early 1700s, many of which became large urban centers (Pittsburgh, Cincinnati, Louisville, etc.). Early on it was recognized that the river supported a diverse assemblage of freshwater mussels. Historically the Ohio River is thus one of the most important rivers in North America to the science of freshwater malacology. It was at the Falls of the Ohio that Rafinesque, one of the most influential (and eccentric) naturalists of the Ohio region, had his epiphany. Thomas Lea, a citizen of Cincinnati, sent specimens to his brother Isaac Lea in Philadelphia, the most prolific freshwater malacologist in North America. Because of the long history of human use, it is not surprising that the river has suffered some indignities. It has been impounded with numerous dams, both for navi-

gation and hydropower (Fig. 1). In more recent times, it has been invaded by the exotic zebra mussel. However, early cities began to impact the river's water quality and mussel fauna long before the arrival of the current dams and the zebra mussels.

That impoundments are detrimental to aquatic life in general, and mussels in particular, has been demonstrated by many case studies (see review of Watters 2000). Perhaps several dozen mussel species in North America, and numerous more freshwater snails, have been driven to extinction by the effects of impoundments (Stansbery 1973, Layzer *et al.* 1993, Lydeard and Mayden 1995). Although mussel faunas change through time, with or without dams, and species become extinct as a matter of course, the interference of humanity has dramatically accelerated this process. For example, the Tennessee River's mussel diversity decreased from 100 species to 44, mainly due to impoundment (Isom 1969). In the Fort Loudoun Reservoir on the Tennessee River, Isom (1971) found only four mussel species, whereas Ortmann (1918) reported 64 species from the same general area before impoundment. The area of the Chickamauga Reservoir of the Tennessee River supported 46 species for perhaps 2000 years

* This is a paper invited by the editor, based on a presentation given at the 2008 AMS meeting in Carbondale. Tom Watters has been responsible for a number of influential papers, some published in the AMB. This paper elegantly shows the effects that urbanization, impoundments, and invasive species have had on unionids in the Ohio River.

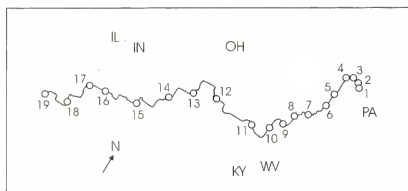


Figure 1. The Ohio River mainstem with locations of dams. 1, Emsworth; 2, Dashields; 3, Montgomery; 4, New Cumberland; 5, Pike Island; 6, Hannibal; 7, Willow Island; 8, Belleville; 9, Racine; 10, Byrd; 11, Greenup; 12, Meldahl; 13, Markland; 14, McAlpine; 15, Cannelton; 16, Newburgh; 17, Myers; 18, Smithland; 19, Olmsted.

prior to impoundment (Parmalee *et al.* 1982). After impoundment, 28 species were extirpated, and several are now extinct. Similar reductions in diversity after impoundment were documented for the Cumberland River (Schmidt 1986, Layzer *et al.* 1993), where the construction of the Center Hill hydroelectric dam resulted in the loss of 78% of the original mussel species. In the Little Tennessee River, only six of the original 50 mussel species at Tellico Lake remained after impoundment (Parmalee and Hughes 1993). The mussels of other rivers have met a similar fate, such as the Kaskaskia River (Suloway *et al.* 1981) and the Tombigbee River (Williams *et al.* 1992).

After impoundment, the original mussel fauna may be eliminated or greatly reduced (Holland-Bartels 1990), or changed in favor of silt-tolerant species, such as anodontines and species of *Leptodea* and *Potamilus* (Clark and Gillette 1911, Ellis 1931, Bates 1962, Isom 1969, Klippel and Parmalee 1979, Parmalee and Hughes 1993, Blalock and Sickel 1996). Thus while some impoundments contain numerous mussels, these invariably are invading, soft-substrate-adapted species that have replaced the original fauna.

In addition to affecting mussels, dams may be physical barriers to mussel hosts as well. Declines in fish diversity due to dams, particularly in migrating fish, have been documented (Branson 1974, Hubbs and Pigg 1976, Steubner 1993, Collier *et al.* 1996). Some mussel populations may no longer be recruiting juveniles because their hosts are absent (Suloway *et al.* 1981, Jones 1991, Burkhead *et al.* 1992). Lowhead dams may be as disruptive as high-lift dams (Dean *et al.* 2002); Watters (1996) showed that dams as low as one meter in height affected host movements and restricted the range of some mussels.

The recently introduced zebra and quagga mussels are highly detrimental to native mussels (Haag *et al.* 1993, Strayer 1999). Zebra mussels compete with native mussels for food,

consume native mussel gametes, interfere with the closure of the native mussels' shells, and result in beach strandings of native mussels (Parker *et al.* 1998). Since their introduction, zebra mussel densities have fluctuated widely in the Ohio River and elsewhere. However, where native and zebra mussels coexist, zebra mussels often result in the local extirpation of native mussels (Gillis and Mackie 1994, Nalepa 1994). For example, native mussels have been nearly extirpated from the western basin of Lake Erie by zebra and quagga mussels (Ecological Specialists, Inc. 1999). Before the current dams were completed and zebra mussels arrived, the Ohio River had been impacted by the rapidly growing urban centers along its length. Unchecked waste water discharge, logging, and mining all contributed to a decrease in water and habitat quality.

Undoubtedly, water quality degradation, impoundments, and zebra mussels have had a negative impact on native mussels in the Ohio River, but the degree and timing of these changes have not been gauged. Fortunately, the Ohio River was sampled extensively by early naturalists and later by professional survey crews. This fact allows us to examine the changes in the mussel fauna of this river over nearly two centuries.

MATERIALS AND METHODS

Historical records

Mussel records were derived from the unpublished database assembled by H. Dunn (Ecological Specialists, Inc.), the survey of Williams and Schuster (1989), the surveys of the USFWS Ohio River Islands National Wildlife Refuge, and the collection records of the Ohio State University Museum of Biological Diversity (OSUM). The river mile, date of operation, and numbers of mussel taxa in each pool are given in Table 1. The presence of mussel species, regardless of year, in each pool is given in the Appendix. Data were not available for individual Pools 52 and 53; these were combined into the Olmsted Pool in this study. The Cairo "Pool" is that area from the confluence to Olmsted and is formed by the impoundment of the Mississippi River backing up into the Ohio River.

Cumulative mussel species richness was based on the assumption that species recorded from a later date had always existed in the pool prior to that survey. For example, a species first recorded in 1980 was considered to have existed in the pool back to 1800. This assumption is based on the nature of mussel surveys in the Ohio River. Prior to intensive sampling beginning in the 1980s the Ohio River had only been sampled by specimen collectors or commercial clambers. These collectors may not have comprehensively sampled any given area, and certainly did not have access to the deeper reaches

Table 1. Ohio river dams included in this study and their maximum recorded mussel species richness. Unlike most river systems, river miles on the Ohio River are numbered from the source (Pittsburgh) to the confluence (Cairo). The “date placed in service” may span the years of first construction of locks to completion of the present dam. Approximate dates are given for the arrival of zebra mussels in each pool. Sizeable population centers are given for each pool. *The Cairo “Pool” is that area from the confluence to Olmsted and is formed by impoundment of the Mississippi River backing up into the Ohio River. N/A, not available.

Dam	Ohio river mile	Date placed in service	# mussel species	Zebra mussel arrival	Population centers
Emsworth	6.2	1919-1922	N/A	1994	Pittsburgh, Pennsylvania
Dashields	13.2	1927-1929	48	1994	
Montgomery	31.7	1932-1936	2	1994	Rochester, Pennsylvania
New Cumberland	54.4	1955-1961	8	1994	
Pike Island	84.2	1959-1965	5	1994	Steubenville, Ohio
Hannibal	126.4	1967-1975	21	1993	
Willow Island	161.7	1972-1976	24	1993	
Belleville	203.9	1963-1968	46	1993	Marietta, Ohio
Racine	237.5	1965-1967	41	1993	Parkersburg, West Virginia
Byrd	279.2	1937	27	1993	Pt. Pleasant, West Virginia
Greenup	341.0	1955-1962	37	1992	Gallipolis, Ohio
					Huntington, West Virginia
Meldahl	436.2	1959-1964	48	1992	Portsmouth, Ohio
					Maysville, Kentucky
Markland	531.5	1959-1964	63	1992	Cincinnati, Ohio
McAlpine	606.8	1961	45	1992	
Cannelton	720.7	1963-1974	40	1992	Louisville, Kentucky
Newburgh	776.1	1969-1975	30	1992	Owensboro, Kentucky
Myers	846.0	1969-1977	35	1992	Evansville, Indiana
Smithland	918.5	1971-1980	35	1992	
Olmsted	938.9-962.6	1928-1929	29	1991	Paducah, Kentucky
(Dams 52, 53)					
Cairo*	confluence	N/A	33	1991	

now accessible by modern scuba techniques, except through the biased sampling of the crow-foot brail, a device dragged behind a boat to snag mussels. Thus many species were missed in earlier efforts that have since been collected. Although some recently collected species may in fact be introductions or taxa increasing their ranges, these species are a small percentage of the overall fauna. *Anodonta suborbiculata* Say, 1831 and *Quadrula aspera* (Lea, 1831) may be the only recent arrivals (Watters, unpubl. data) although soft-substrate-adapted species such as anodontines may be more abundant now than in the past. Because of this, individual pool species richness may be slightly over-estimated.

Based upon the data presented here, the cumulative number of mussel species per pool is plotted as a function of time (Fig. 2). The dates of data for each pool range from 1800 to 2000. The dates of operation of each dam are overlain, as is the general advent of zebra mussels in the Ohio River (beginning in 1991).

RESULTS

The mussel data for several pools were insufficient to draw any conclusions because of a lack of historical records. These pools are not further considered: Byrd, Cairo, Emsworth, Montgomery, New Cumberland, Newburgh, Olmsted, Pike Island, Racine, and Willow Island. Results for remaining pools and averages are illustrated (Fig. 2).

Pool by pool accounts (in alphabetical order)

Belleville

Belleville had among the best historical records of any Ohio River pool, dating back to the early 1800s. Except for a small decline in the 1880s, the diversity had remained fairly constant until the late 1970s, despite the presence of Marietta and Parkersburg in the pool. This decline may reflect the construction of the dam in the 1960s. However, a marked decline

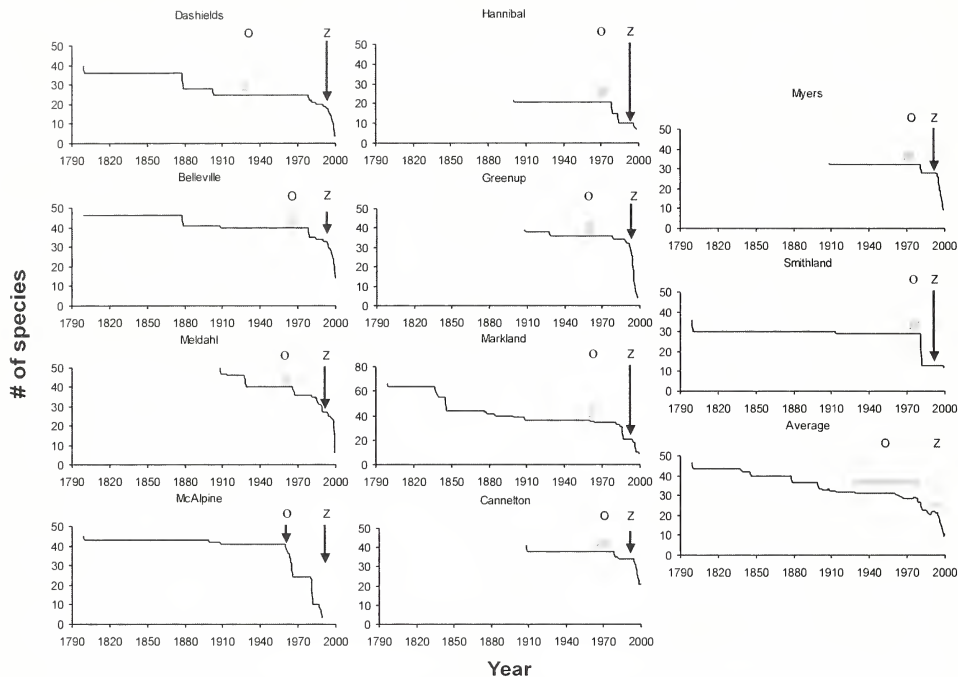


Figure 2. Mussel species richness (y-axis) plotted against time (x-axis) for each Ohio River Pool and averaged across all pools. O, dam placed in operation; Z, arrival of zebra mussels in river. The width of the grey bars spans the years of present dam construction and the arrival of zebra mussels. Pools are arranged from upstream to downstream.

was associated with the advent of zebra mussels. Of the several endangered species recorded from the reach, only *Cyprogenia stegaria* (Rafinesque, 1820) apparently still existed during the last survey.

Cannellton

Cannellton mussel records dated to ~1900 and suggested a robust original fauna of ~40 species. Louisville is at the McAlpine Dam within this pool but there are insufficient data to document its effects, if any. The extinct *Epioblasma torulosa* (Rafinesque, 1820) and other very rare species were found as subfossil material in 2000, but when they were lost from the pool is not known. Most of the fauna persisted until the construction of the dam in 1972, then declined during the late 1970s into the 1980s. However, by comparison, mussel diversity plummeted after the arrival of zebra mussels.

Dashields

The Dashields Pool had one of the longest records of mussels in the river, dating to the 1800s. Data indicated that this reach once supported a thriving mussel community of perhaps 40 species, including the extinct *Epioblasma torulosa*, last seen in 1800. Recent surveys have found fewer than ten species. It is clear that the decline began as early as the late 1800s, undoubtedly due to water quality degradation downstream of Pittsburgh. The dam was not placed in operation until 1929 and no further surveys were conducted until the 1970s. At that time, the pool probably still supported over 20 species. No marked decline attributable to the dam was apparent in the data superimposed as it was on the already existing decline. The fauna dramatically declined with the arrival of zebra mussels in 1991. The most recent fauna was largely comprised of mussels using freshwater drum or

catfish as their hosts. The endangered *Cyprogenia stegaria* probably still exists in the pool.

Greenup

Greenup mussel data showed an alarming decline in diversity after the arrival of zebra mussels—from nearly 40 species to fewer than five. The decline associated with the dam was relatively minor. Huntington and Portsmouth occur in the pool but records were insufficient to demonstrate any loss of diversity as a result. The endangered *Lampsilis abrupta* (Say, 1831) still occurred in this reach in a recent survey.

Hannibal

Mussel data dated from the early 1900s. The negative effects of both dam construction and zebra mussels were evident. No major urban centers exist in the pool. The only endangered mussel recorded from the pool was *Pleurobema plenum* (Lea, 1840), last seen in 1901.

Markland

The Markland Pool may have had more mussel data than any other Ohio River reach. Data were available from the 1800s through 2000, revealing an original mussel diversity probably exceeding 60 species. A marked decline in mussel diversity occurred in the 1840s. The fauna slowly declined to the early 1980s until the construction of the dam. This loss of diversity is probably caused by water quality problems associated with Cincinnati. An accelerated decline occurred at this time, followed by yet another decline when zebra mussels arrived. Numerous rare, endangered, and extinct species once lived in this reach. With the exception of *Cyprogenia stegaria*, apparently still living here, none of these species have been seen in the past 50 years.

McAlpine

Mussel data were available from 1800. The lack of large urban centers in the pool is apparent in the high and continuous level of diversity for over 150 years. The negative effect of dam construction on the mussel fauna was obvious. Mussel diversity had declined dramatically to ~1990, the last date for which we have data. Several rare or endangered mussels were known only as weathered or subfossil shells—*Cyprogenia stegaria*, *Lampsilis abrupta*, *Obovaria retusa* (Lamarck, 1819), *Plethobius cicatricosus* (Say, 1829), *Pleurobema clava* (Lamarck, 1819), and *Pleurobema plenum*.

Meldahl

Mussel data dated to the early 1900s. Over 50 mussel species originally lived in this river reach. Surveys revealed a slow but constant decline in mussel diversity before and after the construction of the dam; the arrival of zebra mussels led to a severe decline in diversity. The early decline may be

attributable to the presence of Maysville in the pool. One extinct mussel once occurred here, *Epioblasma torulosa*, as well as the very rare *Epioblasma obliquata obliquata* (Rafinesque, 1820). Several other endangered species also were recorded from here, but none have been seen in the past 50 years.

Myers (Uniontown)

We had mussel data for the Myers Pool dating back to the early 1900s. Evansville is within this pool but there are insufficient data to document its effects, if any. Mussel diversity seemed to have remained fairly constant until the advent of zebra mussels, with a small decline after dam construction. After the arrival of zebra mussels, mussel diversity precipitously declined. The Myers Pool had two mussel species that are usually considered more southern taxa—*Plectomerus dombeyanus* (Valenciennes, 1827) and *Quadrula aspera*. This pool probably represented the northernmost extent of these species.

Smithland

Records for the Smithland Pool dated to 1800 and clearly showed the impact of impoundment in 1980. Before that time, there does not appear to have been a dramatic decline, testimony to the fact that no large urban centers exist in the pool. After impoundment, the fauna was reduced from its original 36 taxa to fewer than 15. This included the extinct *Epioblasma torulosa* and several endangered species. Effects from zebra mussels were not as dramatic here as in other pools.

Average across all pools

Mussel species richness showed a steady decline from the earliest surveys. The construction of the present dams continued this decline, particularly beginning in the late 1970s when the faunal loss accelerated. This loss quickened with the arrival of zebra mussels.

DISCUSSION

The Ohio River has been sampled for freshwater mussels since at least the 1700s. The records used here date back to 1800 in several instances, providing a lengthy record of mussels in several pools. Prior to impoundment, the average depth of the upper Ohio River was ~0.3 m deep. Frontier accounts clearly depict the upper Ohio River as an often wadeable, meandering series of riffles, runs, and pools (Eckert 1996). Mark Twain (1917: 39) remarked that “We reached Louisville - at least the neighborhood of it. We stuck hard and fast on the rocks in the middle of the river, and lay there four days” and “The Ohio river was friz to the bottom - which

warn't no great shakes in the freezing line, considering that krick aint never got more'n forty barls of water in it, no how." Walt Whitman (1848) reminisced "The bottom of the boat grated harshly more than once on the stones beneath, and the pilots showed plainly that they did not feel altogether as calm as a summer morning."

Mussels in relatively unaltered riverine systems occupy distinct river reaches: some species are most common in riffles and runs whereas others prefer pools and backwaters. This was undoubtedly the case for the Ohio River as well. The construction of dams eliminated the riffles and pools, presumably driving some species (and/or their hosts) to extirpation or even extinction. Most of the currently extinct North American mussel species, predominately in the genus *Epioblasma*, were apparently big river riffle/run species.

The results presented here show a mixed effect of current dams on the mussel fauna. In pools such as Hannibal, McAlpine, and Smithland, the effects are marked. But in other pools comparatively little effect is apparent: Dashiels, Greenup, and Markland, for example. In some cases it is difficult to separate a dam effect from an existing water quality effect. Often the dam effect does not appear to be immediate; in some cases, nearly a decade passes before declines are apparent. This may be due to two causes. First, it may be an artifact created by the timing of the next survey after dam construction. If the next survey occurred ten years after the dam was placed in operation, then the diversity estimate would not have been updated until that time. Second, there may be a biological reason for the lag time. This may reflect the lack of recruitment in some mussel populations while their adults age and eventually die off in the pool. However, there is little evidence for the latter interpretation in the results presented here. Where data are available, there appears to have been an immediate, if often slight, decline in mussel diversity once the current dams were constructed. Once zebra mussels invaded, their impact on native mussels was also immediate.

The current suite of 18 high-lift dams replaced an earlier system of 51 movable wicket and lock dams, although even earlier dams date to 1885. These wicket dams were placed in service in 1929. There is no evidence that they seriously impacted the mussel fauna. This is probably due to the fact that the dams did not permanently impound the river—during normal flow the dams were lowered.

Based upon historical records, we know that most pools supported 20–50 species of mussels; today many have fewer than ten. By contrast, most pools now have 60–80 species of fish (Watters *et al.* 2003). Unlike mussel species, most fish species have persisted in pools for the past several decades. Comparisons with the known potential hosts for the mussels in each pool indicate that the decline of native mussels is not obviously linked to a loss of available hosts. While it is possible

that some very host-specific mussels, perhaps now extinct, may have been affected by the loss of necessary fish, this is probably the exception. Therefore, the loss of native mussels does not seem to be attributable to a loss of hosts, as most pools have a wide variety of fish that could act as hosts to these mussels.

For some pools with extensive chronological data, such as Dashiels and Markland, it is evident that the mussel fauna had already suffered several declines in the 1800s prior to current dam construction. These declines may be associated with the rapid growth and industrialization of the Ohio River corridor in general—logging, mining, discharges, etc. The Dashiels river reach is only 21 km below Pittsburgh and shows a significant decline in diversity beginning nearly 50 years prior to current dam construction. The Markland river reach contains Cincinnati and had been in decline for over 120 years prior to the current dam construction. By contrast, less affected reaches had smaller urban centers; for example, Marietta and Parkersburg are the only sizeable urban centers in the Belleville reach. The Smithland reach is devoid of large urban centers, as is the McAlpine pool, with the exception of Louisville at its extreme downstream reach. For pools having sufficient data, pools lacking urban centers do not show a pre-existing decline in diversity prior to dam construction. Thus, in some cases the completion of the present dams seems to have been part of an ongoing decline originated by other factors associated with urbanization and industrialization, the Markland and Meldahl pools being good examples.

Land surface temperatures in the Ohio Valley have increased since 1880 an average of 0.05 °C/decade, largely after 1980 (National Oceanic and Atmospheric Administration 2009). Although mussel reproductive cycles are believed to be tied to water temperature variation (Watters and O'Dee 2000, Watters *et al.* 2001), the effect of these slight changes is unknown. We do not believe there is any evidence for climatic warming in the Ohio Valley impacting native mussels at this time.

Zebra mussels first appeared in the lowest reach of the Ohio River in 1991 and had spread upstream to Pittsburgh, Pennsylvania by 1994 (U. S. Geological Survey 2009). In nearly all cases the most dramatic declines in mussels are associated with the arrival of zebra mussels in the Ohio River. Often these declines are precipitous. Although zebra mussel densities vary among pools, with upstream pools having the lowest densities, the decline is not associated with river mile. Upstream pools such as Dashiels show the same loss in diversity as do downstream pools such as Newburgh. Regardless of river position, declines due to zebra mussels seem to work on an already decreased diversity caused by impoundment, pollutants, and other factors.

The overall loss of mussels in each pool is rarely attributable to any one cause. Although impoundment clearly has

negatively influenced the overall diversity, zebra mussels appear to have had a more serious and immediate effect. But the decline of Ohio River mussels began nearly 200 years ago and is the result of numerous, synergistic perturbations to the aquatic ecosystem.

ACKNOWLEDGMENTS

We thank Heidi Dunn (Ecological Specialist, Inc.) and Peter Dodgion (formerly U.S. Army Corps of Engineers) for contributing data. Funding for this project was provided by the U.S. Army Corps of Engineers and the Ohio Department of Natural Resources Division of Wildlife. We are further indebted to Mr. Dodgion for overseeing the project and Sarah Hazzard (OSU) and Jennifer Carpenter (OSU) for proof-reading the manuscript.

LITERATURE CITED

- Bates, J. M. 1962. The impact of impoundment on the mussel fauna of Kentucky Reservoir, Tennessee River. *American Midland Naturalist* **68**: 232-236.
- Blalock, H. N. and J. B. Sickel. 1996. Changes in mussel (Bivalvia: Unionidae) fauna within the Kentucky portion of Lake Barkley since impoundment of the lower Cumberland River. *American Malacological Bulletin* **13**: 111-116.
- Branson, B. A. 1974. American paddlefish: Signs of distress. *National Parks and Conservation Magazine* **48**: 21-23.
- Burkhead, N., J. Williams, and B. J. Freeman. 1992. A river under siege. *Georgia Wildlife* **2**: 10-17.
- Clark, H. W. and G. H. Gillette. 1911. Some observations made on Little River, near Wichita, Kansas, with reference to the unionids. *Proceedings of the Biological Society of Washington* **24**: 63-68.
- Collier, M., R. H. Webb, and J. C. Schmidt. 1996. Dams and rivers. *U.S. Geological Survey, Circular* **1126**. 94 pp.
- Dean, J., D. Edds, D. Gillette, J. Howard, S. Sherraden, and J. Tiemann. 2002. Effects of lowhead dams on freshwater mussels in the Neosho River, Kansas. *Transactions of the Kansas Academy of Science* **105**: 232-240.
- Eckert, A. 1996. *That Dark and Bloody River*. Bantam Press Publishers, London.
- Ecological Specialists, Inc. 1999. *Final Report: Unionid Survey in the Western Basin of Lake Erie Near the Bass Islands and Southwest Shore*. ESI Project No. 98-015. O'Fallon, Missouri.
- Ellis, M. M. 1931. A survey of conditions affecting fisheries in the upper Mississippi River. *Bureau of Fisheries, Fisheries Circular* **5**: 1-18.
- Gillis, P. L. and G. L. Mackie. 1994. Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. *Canadian Journal of Zoology* **72**: 1260-1271.
- Haag, W. R., D. J. Berg, D. W. Garton, and J. L. Farris. 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* **50**: 13-19.
- Holland-Bartels, L. E. 1990. Physical factors and their influence on the mussel fauna of a main channel border habitat of the upper Mississippi River. *Journal of the North American Benthological Society* **9**: 327-335.
- Hubbs, C. and J. Pigg. 1976. The effects of impoundment on threatened fishes of Oklahoma. *Annals of the Oklahoma Academy of Science* **5**: 133-177.
- Isom, B. G. 1969. The mussel resource of the Tennessee River. *Malacologia* **7**: 397-425.
- Isom, B. G. 1971. Mussel fauna found in Fort Loudoun Reservoir Tennessee River, Knox County, Tennessee, in December, 1970. *Malacological Review* **4**: 127-130.
- Jefferson, T. 1743-1826. *Notes on the State of Virginia*. J. W. Randolph, Richmond, Virginia [1853].
- Jones, R. L. 1991. Population status of endangered mussels in the Buttahatchee River, Mississippi and Alabama, Segment 2, 1990. *Mississippi Museum of Natural History, Museum Technical Report* **14**. Jackson, Mississippi.
- Klippel, W. E. and P. W. Parmalee. 1979. The naiad fauna of Lake Springfield, Illinois: An assessment after two decades. *The Nautilus* **94**: 189-197.
- Layzer, J. B., M. E. Gordon, and R. M. Anderson. 1993. Mussels: The forgotten fauna of regulated rivers. A case study of the Caney Fork River. *Regulated Rivers: Research and Management* **8**: 63-71.
- Lydeard, C. and R. L. Mayden. 1995. A diverse and endangered aquatic ecosystem of the southeast United States. *Conservation Biology* **9**: 800-805.
- Nalepa, T. F. 1994. Decline of native unionid bivalves in Lake St. Clair after infestation by the zebra mussel, *Dreissena polymorpha*. *Canadian Journal of Fisheries and Aquatic Sciences* **51**: 2227-2233.
- National Oceanic and Atmospheric Administration. 2009. Global climate at a glance. Available at: <http://www.ncdc.noaa.gov/gcag/> accessed 1 June 2009.
- Ortmann, A. E. 1918. The naiades (freshwater mussels) of the upper Tennessee drainage, with notes on synonymy and distribution. *Proceedings of the American Philosophical Society* **57**: 521-626.
- Parker, B. C., M. A. Patterson, and R. J. Neves. 1998. Feeding interactions between native freshwater mussels (Bivalvia: Unionidae) and zebra mussels (*Dreissena polymorpha*) in the Ohio River. *American Malacological Bulletin* **14**: 173-179.
- Parmalee, P. W. and M. H. Hughes. 1993. Freshwater mussels (Mollusca: Pelecypoda: Unionidae) of Tellico Lake: Twelve years after impoundment of the Little Tennessee River. *Annals of the Carnegie Museum* **62**: 81-93.
- Parmalee, P. W., W. E. Klippel, and A. E. Bogan. 1982. Aboriginal and modern freshwater mussel assemblages (Pelecypoda: Unionidae) from the Chickamauga Reservoir, Tennessee. *Brimleyana* **8**: 75-90.
- Schmidt, J. E. 1986. Notes on the historic and present naiad fauna of the Caney Fork River, central Tennessee. *American Malacological Bulletin* **4**: 117.

- Stansbery, D. H. 1973. Dams and the extinction of aquatic life. *Garden Club of America Bulletin* 61: 43-46.
- Steubner, S. 1993. Salmon advocates say the quiet slaughter continues. *High Country News* 25: 1.
- Strayer, D. L. 1999. Effects of alien species on freshwater mollusks in North America. *Journal of the North American Benthological Society* 18: 74-98.
- Suloway, L., J. J. Suloway, and E. E. Herricks. 1981. Changes in the freshwater mussel (Mollusca: Pelecypoda: Unionidae) fauna of the Kaskaskia River, Illinois, with emphasis on the effects of impoundment. *Transactions of the Illinois State Academy of Science* 74: 79-90.
- "Twain, Mark." 1911. *The Writings of Mark Twain: Life on the Mississippi*. 9. Harper & Brothers, New York.
- U. S. Geological Survey. 2009. Welcome to the zebra and quagga mussel information resource page. Available at: <http://nas.er.usgs.gov/taxgroup/mollusks/zebramussel/>; accessed 1 June 2009.
- Watters, G. T. 1996. Small dams as barriers to freshwater mussels (Bivalvia, Unionoida) and their hosts. *Biological Conservation* 75: 79-85.
- Watters, G. T. 2000. Freshwater mussels and water quality: A review of the effects of hydrologic and instream habitat alterations. In: R. A. Tankersley, D. I. Warmolts, G. T. Watters, B. J. Armitage, P. D. Johnson, and R. S. Butler, eds., *Freshwater Mollusk Symposium Proceedings, Special Publication of the Ohio Biological Survey*. Pp. 261-274.
- Watters, G. T. and S. H. O'Dee. 2000. Glochidial release as a function of water temperature: Beyond bradycticty and tachycticty. In: R. A. Tankersley, D. I. Warmolts, G. T. Watters, B. J. Armitage, P. D. Johnson, and R. S. Butler, eds., *Freshwater Mollusk Symposium Proceedings, Special Publication of the Ohio Biological Survey*. Pp. 135-140.
- Watters, G. T., S. H. O'Dee, and S. Chordas. 2001. Patterns in vertical migration in freshwater mussels. *Journal of Freshwater Ecology* 16: 541-549.
- Watters, G. T., T. Cavender, C. J. Myers, M. Kibbey, V. Gordon, B. Pittinger, and T. Pohlman. 2003. *Fish passage study, Product 3 – Distribution of mussels and fish within the Ohio River*. Final Report to the US Army Corps of Engineers, Huntington District. Huntington, West Virginia.
- Whitman, W. 1848. Excerpts from a traveller's notebook. *Daily Crescent* [New Orleans], 10 March. Unpaginated.
- Williams, J. C. and G. A. Schuster. 1989. *Freshwater Mussel Investigations of the Ohio River. Mile 317.0 to Mile 981.0*. Kentucky Department of Fish and Wildlife Resources, Division of Fisheries, Frankfort, Kentucky.
- Williams, J. D., S. L. H. Fuller, and R. Grace. 1992. Effects of impoundments on freshwater mussels (Mollusca: Bivalvia: Unionidae) in the main channel of the Black Warrior and Tombigbee Rivers in western Alabama. *Bulletin of the Alabama Museum of Natural History* 13: 1-10.

Appendix. Mussel species presence by pool. X, species recorded from pool.

Mussel species	Belle	Byrd	Cairo	Cann	Dash	Green	Hann	Mark	McAlp	Medd	Mont	Myers	NewC.	Newb	Olms	Pike	Racine	Smith	Willow
<i>Actinonaias ligamentina carinata</i> (Barnes, 1823)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Alasmodonta viridis</i> (Rafinesque, 1820)								X											
<i>Amblesma plicata</i> (Say, 1817)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Anodonta suborbiculata</i> Say, 1831	X				X	X		X								X			
<i>Anodontoides ferrussacianus</i> (Lea, 1834)								X											
<i>Arcidens confragosus</i> (Say, 1829)			X																
<i>Cumberlandia monodonta</i> (Say, 1829)								X											
<i>Cyclonaias tuberculatus</i> (Rafinesque, 1820)			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Cyprogenia stegaria</i> (Rafinesque, 1820)	X				X			X	X	X						X			
<i>Ellipsaria lineolata</i> (Rafinesque, 1820)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Elliptio crassidens</i> (Lamarck, 1819)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Elliptio dilatata</i> (Rafinesque, 1820)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Epioblasma flexuosa</i> (Rafinesque, 1820)								X											
<i>Epioblasma lewisii</i> (Walker, 1910)								X											
<i>Epioblasma obliquata obliquata</i> (Rafinesque, 1820)								X		X									
<i>Epioblasma personata</i> (Say, 1829)								X											
<i>Epioblasma phillipsii</i> (Conrad, 1835)								X											
<i>Epioblasma torulosa rangiana</i> (Lea, 1838)	X				X			X											

(continued)

Mussel species	Belle Byrd	Cairo	Cann	Dash	Green	Hann	Mark	McAlp	Meld	Mont	Myers	NewC	Newb	Olms	Pike	Racine	Smith	Willow
<i>Epioblasma torulosa</i> <i>torulosa</i>	X		X	X			X		X			X				X		X
(Rafinesque, 1820)							X									X		
<i>Epioblasma triquetra</i> (Rafinesque, 1820)	X			X				X										X
<i>Fusconia ebenus</i> (Lea, 1831)	X	X	X	X	X		X	X	X		X	X	X			X	X	X
<i>Fusconia flava</i> (Rafinesque, 1820)	X	X	X	X	X	X	X	X	X		X	X				X	X	X
<i>Fusconia subrotunda</i> (Lea, 1831)	X		X	X	X	X	X	X	X		X					X		X
<i>Hemistena lata</i> (Rafinesque, 1820)								X										
<i>Lampsilis abrupta</i> (Say, 1831)	X	X		X	X		X	X	X							X		
<i>Lampsilis cardium</i> Rafinesque, 1820	X	X	X	X	X		X	X	X		X	X	X			X		X
<i>Lampsilis fasciola</i> Rafinesque, 1820							X		X									
<i>Lampsilis ovata</i> (Say, 1817)	X		X	X	X		X	X	X		X	X	X			X		X
<i>Lampsilis radiata</i> <i>luteola</i> (Lamarck, 1819)	X	X	X	X	X		X		X			X				X		X
<i>Lampsilis teres</i> (Rafinesque, 1820)		X	X	X	X		X	X	X		X		X			X		X
<i>Lasnigona complanata</i> (Barnes, 1823)	X	X	X	X	X	X	X	X				X				X	X	X
<i>Lasnigona compressa</i> (Lea, 1829)				X			X											
<i>Lasnigona costata</i> (Rafinesque, 1820)	X	X		X	X	X	X		X		X	X				X	X	X
<i>Leptodea fragilis</i> (Rafinesque, 1820)	X	X	X	X	X	X	X	X	X		X	X	X			X	X	X
<i>Leptodea leptodon</i> (Rafinesque, 1820)	X			X			X											
<i>Ligumia recta</i> (Lamarck, 1819)	X	X	X	X	X	X	X	X	X		X	X	X			X	X	X
<i>Megalonius nervosa</i> (Rafinesque, 1820)	X	X	X	X	X		X	X	X		X	X	X			X	X	X
<i>Obliquaria reflexa</i> Rafinesque, 1820	X	X	X	X	X	X	X	X	X		X	X	X			X	X	X

(continued)

Appendix. (continued)

Mussel species	Belle	Byrd	Cairo	Cann	Dash	Green	Hann	Mark	McAlp	Meld	Mont	Myers	NewC.	Newb	Olms	Pike	Racine	Smith	Willow
<i>Obovaria olivaria</i> (Rafinesque, 1820)	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Obovaria retusa</i> (Lamarck, 1819)	X		X	X	X	X	X	X	X	X	X		X	X		X			
<i>Obovaria subrotunda</i> (Rafinesque, 1820)	X		X	X	X	X	X	X	X	X	X	X							X
<i>Plectomerus dombevanus</i> (Valenciennes, 1827)												X							
<i>Plethobasus citricosus</i> (Say, 1829)				X				X	X	X			X	X	X	X	X	X	
<i>Plethobasus cooperianus</i> (Lea, 1834)				X	X			X							X				
<i>Plethobasus cyphus</i> (Rafinesque, 1820)	X		X	X	X	X	X	X	X	X		X	X	X		X	X	X	
<i>Pleurobema clava</i> (Lamarck, 1819)			X					X	X										X
<i>Pleurobema cordatum</i> (Rafinesque, 1820)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Pleurobema plenum</i> (Lea, 1840)			X				X	X	X	X						X	X	X	
<i>Pleurobema rubrum</i> (Rafinesque, 1820)			X			X	X	X	X	X			X	X		X	X	X	
<i>Pleurobema sinuata</i> (Rafinesque, 1820)	X				X	X	X	X	X	X	X	X	X	X		X			
<i>Potamilus alatus</i> (Say, 1817)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Potamilus capax</i> (Green, 1832)												X			X				
<i>Potamilus olivensis</i> (Rafinesque, 1820)	X		X	X	X	X	X	X	X	X		X			X	X	X	X	
<i>Pychochlamys fasciolaris</i> (Rafinesque, 1820)	X		X	X	X			X	X	X					X				
<i>Pygostodon grandis</i> (Say, 1829)	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X
<i>Quadrula aspera</i> (Lea, 1831)			X									X			X				

(continued)

Appendix. (continued)

Mussel species	Belle Byrd	Cairo	Cann	Dash	Green	Hann	Mark	McAlp	Meld	Mont	Myers	NewC	Newb	Olms	Pike	Racine	Smith	Willow	
<i>Quadrula cylindrica</i>	X	X		X			X	X	X			X							
<i>cylindrica</i> (Say, 1817)																			
<i>Quadrula fragosa</i>							X												
(Conrad, 1835)																			
<i>Quadrula metanerva</i>	X	X	X	X	X		X	X	X		X		X	X			X		
(Rafinesque, 1820)																			
<i>Quadrula nodulata</i>	X	X	X	X	X		X	X	X		X		X	X			X		
(Rafinesque, 1820)																			
<i>Quadrula pustulosa</i>	X	X	X	X	X		X	X	X		X		X	X			X		
(Lea, 1831)																			
<i>Quadrula quadrula</i>	X	X	X	X	X		X	X	X		X		X	X			X		
(Rafinesque, 1820)																			
<i>Simpsonioides ambigua</i>		X																	
(Say, 1825)																			
<i>Strophitus undulatus</i>	X			X	X		X		X							X		X	
(Say, 1817)																			
<i>Toxolasma parvum</i>	X	X	X	X			X	X	X							X		X	
(Barnes, 1823)																			
<i>Tritogonia verrucosa</i>		X	X				X	X	X		X		X	X		X		X	
(Rafinesque, 1820)																			
<i>Truncilla donaciformis</i>	X		X	X	X		X	X	X		X		X	X		X		X	
(Lea, 1828)																			
<i>Truncilla truncata</i>	X	X	X	X	X		X	X	X		X		X	X		X		X	
(Rafinesque, 1820)																			
<i>Unionemius tetrasmus</i>	X			X			X	X							X				
(Say, 1831)																			
<i>Utterbackia imbecillis</i>	X	X		X	X		X	X	X		X		X	X		X		X	
(Say, 1829)																			
<i>Villosa fabalis</i>		X																	
(Lea, 1831)																			
<i>Villosa iris</i> (Lea, 1829)	X			X				X		X									
<i>Villosa lienosa</i>																			
(Conrad, 1834)																			
Total # species	46	27	33	40	48	37	21	63	45	48	2	35	8	30	29	5	41	35	24